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ON SOME VARIETIES OF THAIS LAPILLUS IN THE MOUNT DESERT REGION, A STUDY OF INDIVIDUAL ECOLOGY.

BY HAROLD S. COLTON.

INTRODUCTION.

In this study an attempt is made to correlate some of the many color varieties of *Thais* (*Nucella, Purpura*) *lapillus* with the conditions under which the animal lives. The study is based on field work carried out in the neighborhood of Mount Desert Island, Maine, in the summer of 1915. Over 12,000 snails were collected from sixty-seven localities, sorted, and the variations tabulated. These tables were then compared with the environment of the snail.

With respect to *Thais* there is a very general belief that color is correlated with the color of the environment. Cooke (1895) cites a locality in Cornwall where striped forms are found on striped rocks. Blaney (1904) reports yellow forms were found to predominate on the yellow granite rocks of Yellow Island, a small island in Frenchmens Bay on the Maine coast. On account of the great variation of *Thais* and the apparent predominance of one variety in a given locality, a study of the variations might throw light on some of the ecological factors of the sea beach.

LIFE HISTORY OF THAIS.

Thais (subgenus *Nucella* or *Purpura*) *lapillus* is a carnivorous prosobranch mollusk. It feeds almost exclusively in this region on the mussel, *Mytilus edulis,* and the barnacle, *Balanus balanoides.* The former it attacks by boring a hole in the shell about 1 mm. in diameter, devouring the soft parts by means of its long flexible proboscis. The barnacle is eaten in much the same manner, the hole being drilled through one of the scutes. Not only do they sometimes attack the periwinkle, *Littorina littorea,* but will try to bore through the shell of one of their own kind. Although many shells show scars, there is no evidence, however, that many are destroyed in this way.

The descriptive ecologist has neglected the Atlantic coast north of Cape Cod. King and Russell's classification for the coast of Scotland will not hold for this region. Some day, if some one else has not undertaken it, the writer hopes to make a descriptive classification of the animal communities of the sea beach in the Mount Desert region. Provisionally he recognizes the following classification of the Littoral Formation:

- Littoral Formation
  - Solid Rock Association
    - Drift Zone.
    - Littorina rudis Zone (Mean High Water).
    - Balanus Zone.
      (Fucus Zone.)
    - Mytilus Zone.
    - Transition Zone (Mean Low Water).
  - Rock Association.
  - Rock Pool Association.
  - Boulder Association.
  - Shingle or Pebble Association.
  - Sand Beach Association.
  - Mud Flat Association.

The mean rise and fall of the tide is ten vertical feet.

Thais is found in the Solid Rock, Boulder and Rock Pool Associations. In the two former it is confined to the Balanus, Fucus, and Mytilus Zones, and particularly to the Balanus and Mytilus Zones, as there the food is found. There, *Thais* is associated with *Littorina rudis, L. palliata, L. littorea, Balanus balanoides* and *Mytilus edulis.* When the tide is high the cunner (*Tautogolabrus adspersus*) and the pollack (*Pollachius virens*) invade this formation to feed.

Thais is not found in the Shingle, Sand or Mud Flat Associations. Nor is it found alive in any association of the Bottom Formation, unless we should classify the Rock Pool as a detached part of this formation.

It is not found in any stratum other than the upper surface of rocks. It is found therefore neither on the weeds nor under the soil.

Its habitat is very closely associated with its food. (See diagram, fig. 1, illustrating the food relations of *Thais* to its organic environment.)

The eggs are laid in little urn-shaped capsules in sheltered places. They are more abundant in the Mytilus Zone in favored spots, such as in cracks in the rocks or under masses of *Fucus* than in the Balanus Zone. In each capsule about 400 eggs are laid. As cannibalism is practised (Beard 1899, Carpenter 1857, Glaser 1905, Pelseneer 1904, Robert 1902) by the growing snail, a capsule containing snails ready to hatch will hold but 8–14.

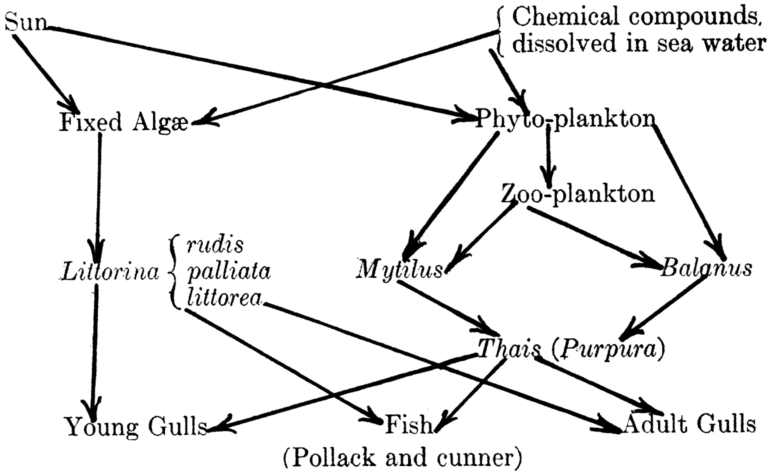

Fig. 1.—Diagram illustrating the principal relations of *Thais* to its organic environment in the Rock Association. To be complete this diagram should show an entire cycle of the material. Each one of the organisms listed above gives off liquids to the sea water that may be again used. They also furnish solids either as waste products or by death, which, when acted on by bacteria, will give more soluble matter as well as a residual solid that will help contribute to the sea bottom in other localities. The dead animals will supply food for amphipods, the amphipods food for fishes like the sculpin, and so relations are established with other associations. This diagram shows that the biota of the Rock Association is dependent alone on the palagic formation. The relationships with other associations are destructive to it rather than constructive.

The young snail has enemies in the shape of fish, so those which fail to take refuge in small cracks in the rocks are destroyed. At this time the food consists of young mussels which grow abundantly in the joints in the rocks. If one does not know where to look for the young snails, none will be seen, so far are they crowded into the cracks.

A few pollack that were caught at high water over a Thais habitat had their stomachs full of young *Littorina palliata* which they had eaten from the same locality in which *Thais* lives. *L. palliata* cannot hide in the rock cracks, as their food is on the Fucus stems. If the fish could find young *Thais*, there is no reason why they should not be eaten as well as *Littorina*.

Although the young snails are hatching throughout the greater part of the summer, most of them hatch out in August and reach between 10–15 mm. in the first winter. This is measured by large ridges on the shell, which indicate periods of rest in the growth of the shell. These rest periods are assumed to indicate the winter, but are not proved to correspond to it.

The curves in fig. 2 show the rate of growth in three different environments. These are but approximations. Further study may show that the first year may be really the second.

The oldest snail found was estimated as being seven years old. The great majority are about two or three years old.

Cooke (1895) estimates that each female snail lays two hundred egg capsules a year. Each capsule contains about four hundred eggs. Food seems to be in most places abundant. The snails have been observed to be limited in number by the following factors:

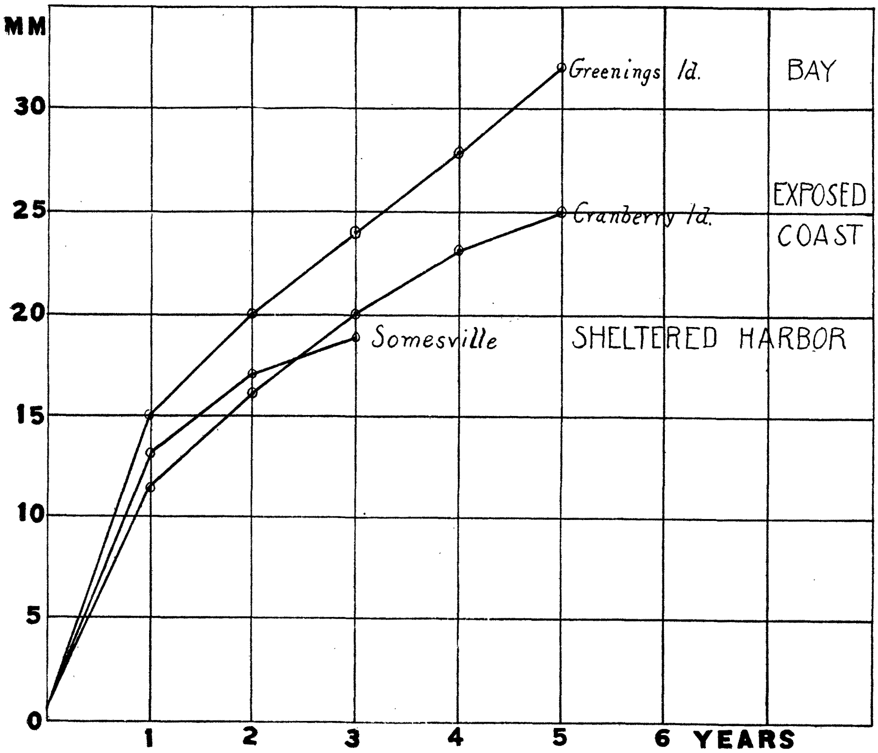

Fig. 2.

(1) Cannibalism within the egg capsule, only ten to twelve hatching out of 300–400 eggs.

(2) Limit to the number that can take refuge in cracks in rocks and yet get enough to eat.

(3) Fish, such as pollack, will gobble up any stragglers.

(4) Half-grown snails, ones too big for the pollack, are used by herring gulls as food, the empty shells being regurgitated.

(5) Very large specimens are carried by the gulls to a height and dropped on any near-by flat rock in the same way as the gulls treat both sea urchins (*Strongylocentrotus*) and welks (*Buccinum*). Only the largest *Purpura* will break and only the largest are collected for this purpose.

(6) Certain ones seem to be parasitized by a sporocyst, but this was not investigated.

(7) Accidents, such as a surf heavy enough to move the rocks on which the animals live, may destroy others. In such habitats few if any are found. The maximum size of these rocks may in exposed places be boulders two to three feet in diameter, while in very sheltered places *Thais* will be found on pebbles two inches in diameter. The limit is obviously determined by wave action.

(8) Ice probably destroys others, as they are not found in places where shore ice can accumulate.

(a) In Maine they are not abundant in shallow coves that freeze up solid in the winter time.

(b) Their geographical distribution also seems to indicate that sand beaches are a barrier, as *Thais lapillus* is not found west of Montauk Point. On Long Island Sound the barrier has not been determined. Both *Balanus* and *Mytilus* being found west of Stamford, Conn., the most westerly recorded station for *Thais*, and the shore is still rocky. In the north shore ice seemed to form the barrier See map, fig. 3.

Various adaptations are at once manifest on examining this animal: (1) The strong shell, so strong that a drop from a height will not always break it. (2) The strong foot, which makes dislodgment from its substratum difficult. (3) Its habit of seeking shelter under rocks and fucus. (4) The method of egg-laying, with its protection of the young until they are able to care for themselves, although if but two and a quarter per cent. of these laid hatch, those two and a quarter per cent. are almost sure to hatch.

METHOD.

As each station was visited, from 200 to 500 shells were collected when *Thais* was abundant. In some places they literally covered every inch of the rock. In other places they were so rare that a careful search of a quarter of a mile of beach would often disclose but two or three.

Each collection as made was placed in a bag made of mosquito netting. While still alive the snails were sorted into the dozen or so groups of the principal varieties. The number in each group was tabulated. For future reference the bag of snails was preserved in a tub of formalin.

A study of the color varieties seems to show that there are a number of colors and patterns that may be combined together in any sort of way. These are as follows:

(1) Pure white shells that show no trace of color.

(2) Purple. The color in this case is diffuse through the shell, but is darker within the aperture.

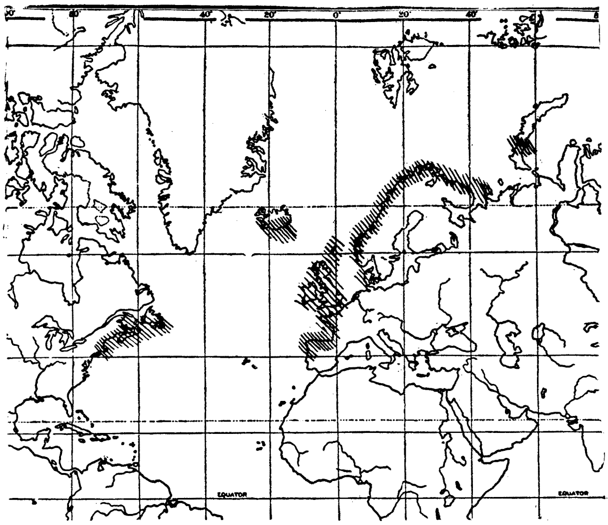

Fig. 3.—Map of the North Atlantic Ocean showing the distribution of *Thais* (*Purpura* or *Nucella*) *lapillus*. (After Cooke, Proc. Mal. Soc. London, vol. II, p. 193.) The cross-hatching shows the occurrence of *T. lapillus*. The southern barrier to *T. lapillus* is not clear, but the northern barrier is obviously the presence of ice on the shore.

(3) Chestnut. This color may be pure quite often, but it is usually combined with purple, forming a chocolate, or with yellow, forming olive.

(4) Yellow is a color which, when uncombined with one of the others, makes the shell very conspicuous on the rocks. Owing to its relative rarity and to its being so conspicuous, it often appears in shell collections in proportions that are misleading. Only by collecting all the snails from a given locality can this be avoided.

(5) *Dilute*. Every one of the colors mentioned above may appear in a dilute in contrast to its intense form.

(6) *White lip* of the apperture is quite common in some localities. In fact, purple is rarely found not associated with a trace of lighter color on the lip. This *white lip* may be combined with all colors and dilutions.

(7) *Narrow stripes.* In many shells about ten narrow white stripes are found on any color background. These are sometimes associated with the ridges which appear on many shells.

(8) *Wide stripes* of white, usually two in number, often appear. The widest stripe equals two or three of the narrow ones and the smaller stripe is double the width of the narrow ones. The widest stripe is always posterior to the narrower stripe.

(9) *Spot of purple* on the columella. This is rare at Mount Desert, but very common at Rye Beach, New Hampshire.

(10) *Imbricata.* A fluting of the ridges of the shell gives rise to the variety called by Lamarck *imbricata.*

Apparently each one of the ten characters recognized may be combined with any other. If this is so there must be 1,103 varieties. Not that many varieties have been found. This is due to the fact that one cannot distinguish certain combinations from one another. As an example, let us consider the case of the colors alone. We have purple, chestnut, yellow, and white. There are eight possible combinations of these: white, purple, chestnut, yellow, purple-chestnut, purple-yellow, chestnut-yellow and purple-chestnut-yellow. These last four are shades of olive and chocolate, and cannot be distinguished easily from one another. If we combine these four color combinations into one group and omit the white lip and purple spot on the columella, we will reduce the possible number of variations to be recognized from 1,103 to 33. Twenty-eight of these thirty-three varieties have been recognized. However, there are five that are so rare that they were not discovered in a collection of six thousand shells when they were particularly sought after. These were narrow stripe dilute yellow, wide stripe narrow stripe yellow, wide stripe narrow stripe dilute yellow, narrow stripe dilute olive, and wide stripe dilute olive. The yellows which contribute to the olive color and the dilute are much rarer than any of the others, so it is no wonder that they are the ones that would be lacking in combinations.

It is obviously impossible to attempt to correlate all the known varieties with environmental factors, so the writer has for the sake of convenience reduced still further the number of groups. The particular groups recognized are as follows:

(1) White; that is, pure white.

(2) Light—pure white, together with intense and dilute chestnut with white lip. The outer layer of the shell of these is white.

(3) Dark—chestnut and purple in all their combinations.

(4) Yellow—pure yellow.

(5) Striped—both narrow and wide stripe in all their combinations and color.

(6) Imbricated—in all the combinations of patterns and colors.

In the tables that follow the number of snails found in each group is stated in per cent. of all the snails in each collection from a given station.

THE RELATION OF THE VARIETIES TO THE ENVIRONMENT.

The base for this study was Greenings Island, an island located between Northeast and Southwest Harbors in the mouth of Somes Sound. It is triangular in shape, with a perimeter of about two and a quarter miles. The main mass of the island is composed of till, which at one time formed the terminal moraine of the continental glacier before it retired from Somes Sound. This till is protected from rapid wave erosion by outcrops of reddish granite at the east and west end of the island. This granite is cut in several places by broad basalt dykes which run in a general north and south direction. Under wave erosion the till between the outcrops of solid rocks has given material to form a boulder-strewn beach and in favorable places the finer products have given rise to pebble and sandy beaches. On the west or more sheltered side of the island between the granite outcrops are a number of muddy coves.

On this small island we have all the principal Littoral associations present. The distribution of these are found in fig. 4. This figure is a diagram of the shore of Greenings Island, with the vertical scale very much exaggerated. It has been made as though the shore were cut at the northwestern point and folded out so that this northwestern point appears at each end of the diagram. The character of the shore is indicated. The island as a whole is protected from heavy surf by outlying islands, but the eastern end is exposed to the ocean swell from both the south and east, and at times of storms is subject to quite a surf. The northeast shore and south shore are relatively unprotected at the east end, but become more protected toward the west. On the diagram the per cent. of pure white shells are placed in the locality in which the collection was made.

An inspection of this figure will show that the most unprotected portion has the lighest colored snails, while the portion of the island

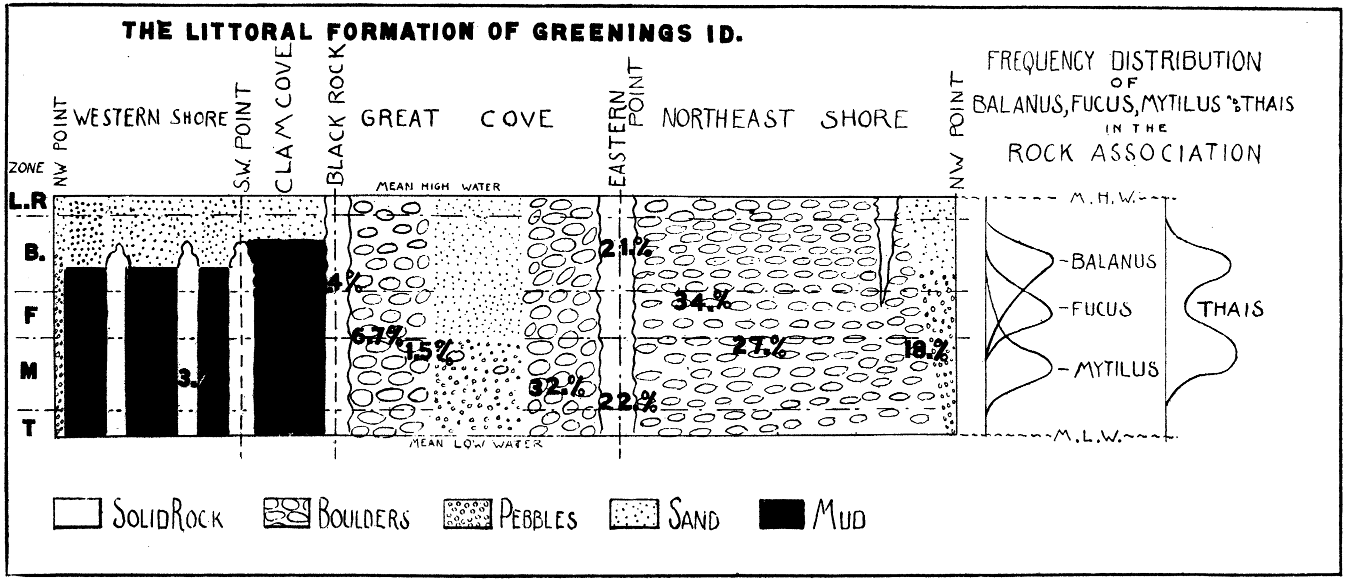

Fig. 4.—Diagram of the beach of Greenings Island, Maine. This is drawn as if the shore of the island were cut at the northwestern point and beach folded out into a straight line. The length of the diagram represents two and a quarter miles. The width represents the space between mean low tide and mean high tide, which is equal at this place to ten vertical feet.

The percentages on the diagram refer to the per cent. of white *Thais* found at each locality. It shows how the number of white are most abundant at the eastern end and fewest at the western.

L. R., Littorina rudis zone; B., Balanus zone; F., Fucus zone; M., Mytilus zone; T., Transition zone.

subject to the smoothest water has the darkest. This difference is very striking and the intermediate stations show intermediate ratios.

This has led the writer to classify the shores according to the waves. These are arbitrary divisions and of course every intergradation is found, but in most cases there is very little hesitation how a given station should be described. If a great uncertainty exists, the station was placed in both classes.

Sea cliff or surf exposed to the open sea. An ordinary row boat can practically never land with safety.

Bay exposed to a moderate surf during high winds. Except at those times a small boat can easily land on the shore without danger of accident.

Harbor so smooth that a row boat can practically always make a landing.

In the tables which follow the stations nearest together are always compared.

Table I.

Locality.	Condition.	Station No.	No. of Individuals.	% Lt.	% White.
Bakers Id	Surf.	23	65	6.1	0
	Bay.	24	167	20.7	6
Seal Harbor	Surf.	54	176	2.8	0
	Bay.	56	34	55.6	44
Cranberry Id	Surf.	10	319	30	4.3
	Surf.	11	195	59	9.7
	Bay.	13	204	15	5.7

We can conclude that in general the snails on the most exposed situations are darker than those found in the bay.

Table II.

Locality.	Condition.	Station No.	No. of Individuals.	% Lt.	% White.
Greenings Id	Bay.	2	516	44½	21½
	Harbor.	31	333	10	1½
Buckel Id	Bay.	15	234	63	36
	Harbor.	16	218	13½	5½
Bear Id	Bay.	43	277	24	12½
	Harbor.	44	67	10½	1½
Orono Id	Bay.	19	55	11	7
	Harbor.	18	184	50	27
Southwest Harbor	Bay.	37	194	29½	19
	Harbor.	36	196	10½	5½
	Harbor.	35	273	25½	11
	Harbor.	47	172	14½	6½

If we combine the conclusion from Table I with Table II we see that snails in the exposed positions tend to be dark as well as those in the sheltered places, while those in the bay shore tend to be the lighter colored.

The following table includes the results of collections made at stations separated by no barrier, near together, but on a substratum of different colored rocks. The numerous black basalt dykes that everywhere cut the red granite make a number of collections of this sort possible. Only a very few of the possible ones have been studied.

Table III.

Locality.	Condition.	No. of Station.	No. of Indiv.	% Lt.	% White.	% Yellow.
Greenings Id., east end.	Red rocks, 1000 ft. to Sta. 2.	25	316	57	34	6.3
	Black rocks, 20 ft. to Sta. 50.	2	516	44	21	0
	Black rocks, 500 ft. to Sta. 21.	50	160	37	22	0
	Red rocks,	21	164	47	32	.6
Greenings Id., southwest end.	Red rocks, 200 ft. to Sta. 28.	31	333	10	1.5	2.1
	Black rocks, 50 ft. to Sta. 30.	28	247	14	6.7	1.2
	Black rocks,	30	289	2.9	.4	3.8
Suttons Id.	Red rocks, 110 ft. to Sta. 8.	9	159	35	2.5	7.5
	Red rocks, 150 ft. to Sta. 7.	8	135	28	2.2	31.8
	Black rocks.	7	123	19	0	18.7

In general, more light-colored snails are found on the red rocks than on the black rocks. The association of yellow forms with the environment is inconclusive. There does not seem to be any correlation from these few cases. Thirty-three collections from red rocks average 4% yellow. Fifteen collections from black rocks average 4.7% yellow.

In this region there are occasional outcrops of a banded rock, a chlorite schist. That there might be a correlation between striped forms and schist is a possibility that may be investigated. The collections from the red granite given in the table are those made nearest to the chlorite schist. This comparison was not in mind when the collections were made, so the stations are often several miles apart.

TABLE IV.

Locality.	Substratum.	Striped Shells.
Blue Hill Bay	Chlorite schist	1.1%
	Red granite	9.8%
Western Way	Chlorite schist	27 %
	Red granite[1] (average of 18 collections from this region)	14.4%
Western Way	Chlorite schist	27 %
Nearest Granite Station	Red granite	18.5%

The distance apart of the stations introduces so many other factors that with such meagre data no conclusions can be drawn. The writer expects that the results are really negative.

The relative proportions of the imbricated forms from different localities are as follows:

In the upper bays the water is much warmer than near the ocean. This warmth is indicated at Blue Hill by bathhouses being located along the beaches. None of the resorts farther down the bays have any, the water being too cold for bathing in the bay in those places. The upper bays are relatively shallow and there are muddy spots found on the rocky beaches between the rocks. Five stations in this region had imbricata ranging from 38% to 96%.

In the middle bay region of Blue Hill Bay the water is deep and the rocky shores are clean. No imbricata were found in the three stations in this region.

The western side of lower Blue Hill Bay is shallow, with many islands and ledges. Among these islands there are many mud flats, and the same conditions are found on the upper bay. Five stations had *imbricata* ranging from 9% to 30%.

Near the islands separating the lower bay from the ocean the water is, in general, deep and the rocky shores clean. Five stations, 0–5½% *imbricata.*

On the outer islands the surf, of necessity, keeps the rocks free from sediment. Two stations, 17–57%.

In Somes Sound environmental conditions similar to those in Blue Hill Bay are found. The rocks are muddy in the harbors near mud flats and clean where wave action is possible and the water is deep. If we except two stations at the Southwest Harbor steamboat wharf, where the ratio of *imbricata* was 19% and 19.2%, respectively, the average of thirty-five stations containing 7,119 individuals was only .47%. The largest number found was but $3\frac{1}{2}\%$ at any one station and that was on the rocks of a muddy harbor. The station in Somes Harbor farthest away from the ocean had but .6% *imbricata.*

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[1] Of these eighteen collections, four had over 27% striped, one had 37% striped.

That there are other geographical factors is shown by the rarity of *imbricata* in the Somes Sound region. Very few are found in exposed situations on the Cranberry Islands and on Seal Harbor Head, situations exposed to the full effort of the surf. Except for a colony at the Southwest Harbor steam-boat wharf, in the whole Somes Sound region they are indeed rare. Out of 2,765 shells collected on Greenings Island but three were imbricated and these three were found at one station on the muddy west side of the island.

However, in general, we can say that the imbricated forms are found in greatest abundance in exposed situations, as Duck Island and Long Island, and also in the most sheltered positions.

Most of the varieties found in the Atlantic are also found in the forms inhabiting the north Pacific Ocean. Dall[2] reports that the lamellated forms of *Thais* in that region are found best developed in sheltered harbors. The Atlantic lamellated forms we have seen may occur in sheltered as well as in exposed situations.

As *Thais* is found in both the Balanus and the Mytilus Zones, is there any difference between collections made close together but in different zones? The answer to this question is summed up in the following table (Table V) compiled from collections made but a few feet apart, but in different zones.

TABLE V.

Locality.	Zone.	Sta.	Lt.	Wt.	Yel.	St.	Imbricata.
Greenings Id., eastern point	*Balanus.*	2	44.5	21.3	0	?	0
	Mytilus.	50	37.5	22.5	0	14.4	0
Steam-boat wharf, S. W. H.	*Balanus.*	37	29.5	19.	17.5	1.5	19.0
	Mytilus.	47	14.5	6.4	4.1	37	19.2
Stanley House wharf, S. W. H.	*Balanus.*	35	25.3	11	2.2	4.0	0
	Mytilus.	34	21.4	4.8	0	5.3	0

(1) There are more light forms in the white Balanus Zone than in the dark Mytilus Zone.

(2) There are fewer yellow forms in the dark Mytilus Zone.

(3) Striped forms not conclusive.

(4) Imbricated forms not affected.

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[2] *Proc. U. S. Nat. Mus.*, vol. 49, pp. 557–572.

NATURAL SELECTION.

Natural selection, we can assume, is most severe on Little Duck Island. This little island, lying four miles out at sea, is exposed to the surf on every side. The herring gull, one of the chief enemies of adult *Thais*, has a rookery on the island, and every summer thousands of birds roost there at night and have their nests. Everywhere regurgitated Thais shells cover the rocks, which tell a story of a struggle for existence.

In collecting on this island for two hours but four hundred and twenty-nine living snails were found. These were discovered at the lower edge of the Mytilus Zone. All had been picked off the rocks above by the gulls. This collection is chiefly notable in containing a very large proportion of dark individuals, only 1.1 per cent. white were found. Nineteen per cent. were imbricated.

It can be said with justification that where the struggle for existence is greatest on the exposed islands and the muddy harbors selection tends to preserve the dark-colored and the lamellated forms.

CONCLUSIONS.

A study of the color varieties leads one to the conclusion that they are hereditary and that we are dealing with things that are probably unit characters. Even the development of lamellæ, as in *imbricata*, are not modifications caused by induction that is caused by the direct action of the environment.

As there are great differences between the ratio of the color varieties present in different localities, we assume that natural selection is acting.

In the bay environment conditions are at an optimum. No mud film covers the Mytilus, and Balanus forms crusts over the rocks an inch to an inch and a half thick. Here *Thais* is most abundant. Five hundred can be gathered in ten minutes or even less. A handful can be gathered at one scoop.

In the surf environment the barnacles do not form such thick crusts. On the harbor shore ice destroys the barnacles in the winter and a mud film covers the mussels. So that the barnacles are usually small and far apart, while the mussels are separated by mud from the rocks. Sand and mud are barriers to *Thais*. Although the surf environment and the harbor environment are the antithesis of one another, yet they have many effects on *Thais* that are similar. These effects are as follows:

(1) The curve of growth, fig. 2, shows that those in the surf environment at a given age are smaller than those from the bay environment.

(2) There is a tendency toward dark individuals.

(3) There is a tendency toward lamellated forms.

These studies show that natural selection has some determining action on the color varieties present. (1) It has been shown that the color of the rocks, whether dark or light, has an effect. (2) It has been shown that the white barnacle-covered rocks contain more light-colored ones than those on the mussel bed but a few feet away. (3) It has been pointed out that those living on rocks near mud flats are darker than on the more exposed points of the same islands.

The present study must leave the question of the relation of the yellow forms and the striped forms to the color of their substratum yet unsettled.

In general, however, there is a relation between the color and the environment. This relation is caused by natural selection and not by the direct action of the environment.

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